A NEW CRAB FAMILY FROM THE VICINITY OF SUBMARINE THERMAL VENTS ON THE GALAPAGOS RIFT (CRUSTACEA: DECAPODA: BRACHYURA)[1]

Austin B. Williams

Abstract.—*Bythograea thermydron,* a new genus and new species of brachyuran crab, is described from the vicinity of submarine thermal vents on the Galapagos Rift. About 160 of the crabs in various states of maturity were collected by means of baited traps, suction, and mechanical arm with the aid of the deep submersible, *Alvin. Bythograea* represents a new family that exhibits some characters of the families Portunidae and Xanthidae, with superficial resemblance to the family Potamidae s. l. It is placed in an independent superfamily.

Introduction

The Galapagos Rift zone supports a community of organisms living on hard bottom within and somewhat beyond the influence of thermal vents in the ocean floor. Investigators aboard the deep submersible *Alvin* viewed and photographed these organisms, taking a few samples in February and March 1977 (Corliss and Ballard, 1977; Corliss *et al.,* 1979), and on a second expedition in February 1979, secured far more abundant samples of the biotic community among which were numerous adult brachyuran crabs taken in baited fish traps and a few megalopae associated with mussel clumps (Grassle *et al.,* 1979; Ballard and Grassle, 1979). Further observations were made and a few specimens collected during a third expedition in November–December 1979. The crabs are here described.

I am greatly indebted to J. F. Grassle, Woods Hole Oceanographic Institution (WHOI), chief scientist on the second and third expeditions, for transmitting to me the material on which the description is based as well as observations from the submersible, and to his associates L. Morse-Porteous and I. Williams for assistance in laboratory study of the crabs; to D. M. Cohen, National Marine Fisheries Service, Systematics Laboratory, National Museum of Natural History, whose traps baited for capture of fishes were the adult crab collectors, not only for that good fortune but also for his observations on crab sizes, distribution and behavior; and to J. R. Chil-

dress, University of California, Santa Barbara, who contributed observations on color as well as a megalopa for study. F. A. Chace, Jr., D. M. Cohen, and R. B. Manning critically read the manuscript. I thank M. R. Carpenter, National Museum of Natural History, for photographing the specimens, and María Dieguez for carefully preparing the drawings and photographic plates.

Superfamily, Bythograeoidea, new superfamily

Carapace flattened. Antennules folding transversely, basal articles contiguous, antennular septum absent. Mouth field slightly diverging anteriorly. Sternum broad. Chelipeds with fused basis-ischium. Megalopa crablike, carapace broader than long.

Family, Bythograeidae, new family

Adult characters.—Front of moderate width. Supraorbital border present. Stalked eyes movable, cornea unpigmented. Antennae inserted below eyestalks, peduncular articles slender. Carpus of third maxilliped articulating near anteromesial corner; endognath of first maxilliped with mesial lobe. Male openings coxal, female openings sternal.

The family contains only the following genus.

Genus, *Bythograea*, new genus

Carapace transversely elliptical, regions indistinct; anterolateral region produced, spineless. Front of moderate width, slightly produced and bilobed. Orbits incomplete; supraorbital margin short in adult; suborbital plate nearly horizontal and almost fully visible in dorsal view in adults and subadults, but incompletely developed in early crab stages. Third maxillipeds with long, setose palp. Chelipeds moderately unequal, hands inflated; walking legs with dactyls pointed. Male abdomen with segments 4 and 5 partly fused; mature female abdomen broad, segments free, biramous pleopods on 2–5.

Type-species.—*Bythograea thermydron*, new species.

Name.—From the Greek, "bythos," the deep, the depths of the sea, and "graia," sea crab (Liddell and Scott, 1940). The gender is feminine.

Bythograea thermydron, new species
Figs. 1–11

Material.—Thirty-six ♂ and 100 ♀ from dives of the *Alvin* on 3 vent areas along the Galapagos Rift: Dive 880, Mussel Bed, 21 January 1979, 0°48.89′N, 86°09.12′W, 2493 m, 1♂; Dive 887, Mussel Bed, 12 February 1979, 2488 m, 19♂, 4♀; Dive 888, Mussel Bed, 13 February 1979, 2483 m, 12♂, 29♀ (2

ov); Dive 890, Rose Garden, 15 February 1979, 0°48.25′N, 86°13.48′W, 2447 m, 24 ♀ (2 ov); Dive 894, Rose Garden, 19 February 1979, 2457 m, 6 ♀; Dive 895, Rose Garden, 20 February 1979, 2482 m, 1 ♂; Dive 896, Rose Garden, 21 February 1979, 2460 m, 3 ♂, 36 ♀ (2 ov); locality unrecorded, 1 ♀.

The following are designated and labelled as types deposited in the crustacean collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C.: 172830, holotype ♂, Dive 887; 172831, allotype ♀, Dive 896; 172832, paratypes, 4 ♂, 1 ♀, Dive 887; 172833, paratypes 2 ♂, 4 ♀, Dive 896. To be transferred from the USNM collection are the following paratypes: 1 ♂, Dive 887, 1 ♀, Dive 890, to the Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; 1 ♂, Dive 887, 2 ♀, Dive 890, to the Allan Hancock Foundation, University of Southern California, Los Angeles, Calif.; 1 ♂, Dive 887, 2 ♀, Dive 890, to the British Museum (Natural History), London; D32621, 1 ♂, Dive 888, D32622, 2 ♀, Dive 890, to the Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; 1 ♂, Dive 887, 1 ♀, Dive 890, to the Museum National d'Histoire Naturelle, Paris, France.

Remaining specimens are at the Woods Hole Oceanographic Institution.

Description.—General aspect cancroid, depressed. Carapace broad, transversely elliptical, its rounded lateral angles displaced somewhat anteriorly; almost flat in middle dorsally, very slightly arched from anterior to posterior and near lateral margins; anterolateral region produced, margin not toothed; surface finely granulate anteriorly and laterally, smooth but minutely punctate to unaided eye over posterior ⅔ to ¾; regions indistinct. Frontoorbital width ca. ¼ carapace width.

Front obscurely bilobed; median depression shallow; projecting over folded antennules and somewhat deflexed; margin entire, usually slightly concave mesially and beaded with line of fairly uniform sized, low and flattened, sometimes coalesced, often dark tipped granules (neither dark tipped nor flattened in white female allotype); transverse submarginal row(s) of smaller similar granules merging with marginal row at inner corner of short supraorbital margin and continuing laterad past deeper outer orbital notch, arching forward slightly to merge with anterolateral margin running from beneath eye along edge of suborbital plate posterolaterally to broadly rounded lateral angle, edge of margin beaded with nearly uniform, close-set, low and flattened, often dark-tipped granules (forward trending in females); tract of forward trending, often dark-tipped (unpigmented in female) granules lying between double row at frontal margin with its lateral extensions and line(s) of smaller, more closely spaced similar granules posterior to it; tract sweeping submarginally along anterolateral border and narrowing to disappear near lateral angle (i.e. along undifferentiated frontal, orbital, hepatic and anterolateral regions); still other similar granules behind this tract most

prominent near anterolateral margin and on anterior gastric region. Carapace with almost smooth part behind these anterior areas microscopically granulate anteriorly grading posteriorly into network of exceedingly fine lines and finally into almost featureless surface near posterior margin, network of fine lines also among anterior and anterolateral granules. Regions (proto-, meso-, metagastric, cardiac, cf. Renaud, 1977) dimly indicated; faint, thin, serpentine line of obsolescent granules in extremely shallow epibranchial groove in male (groove absent in female) originating posterior to lateral angle at each side and curving anteromesially over branchial region, then posteromesially toward mesogastric region. Posterolateral margins convergent, slightly sinuous above bases of fifth legs. Posterior margin concave, slightly beaded with granules and paralleled by submarginal groove becoming more pronounced above fifth legs.

Subhepatic and subbranchial regions ornamented with often dark-tipped granules in males, usually unpigmented in female, coarsest along hepatic region but becoming finer and more numerous near base of chelipeds, line of fine granules along lower subbranchial margin defined by pleural line. Males with dense mat of soft plumose hairs in narrow tract below posterior part of anterolateral margin and along posterolateral margin, with continuation on subbranchial region, and protruding somewhat between bases of legs; females with shorter more restricted patch on subbranchial region.

Orbits highly modified and almost non-existent; short supraorbital margin bearing 2 or 3 often dark-tipped granules; mesial corner of outer orbital area forming recess lined with hairs for reception of cornea; lower margin occupied by subtriangular suborbital plate almost fully visible in dorsal view, slightly exceeding front and tilted slightly anteroventrally from frontal plane, lateral to and almost at same level as epistome, and separated from polygonal, narrow but transversely broadened, granular outer orbital area by prominent oblique uncalcified suture disappearing laterally; suborbital plate separated mesially from epistome by articular membrane, large irregular operculum covering opening of antennal gland, and fixed basal antennal article.

Eyestalks reduced, projecting anterolaterad, movable, depressed and

→

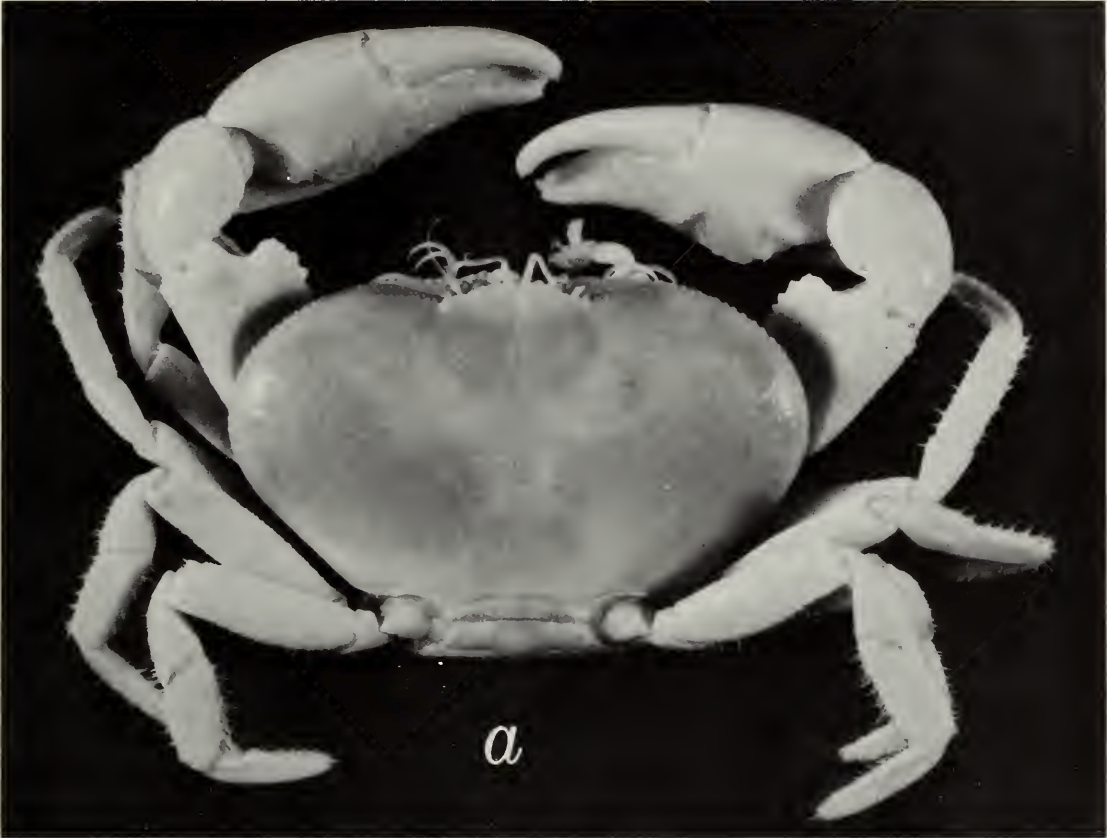Fig. 1. *Bythograea thermydron.* Male holotype: **a,** Dorsal view; **b, c,** Right and left chelae in external view. Scale = 1 cm.

Fig. 2. *Bythograea thermydron.* Male paratype USNM 172832, left first and second walking legs missing: **a,** Dorsal view; **b, c,** Right and left chelae in external view. Scale = 1 cm.

Fig. 3. *Bythograea thermydron.* Female allotype: **a,** Dorsal; **b,** Ventral view. Scale = 1 cm.
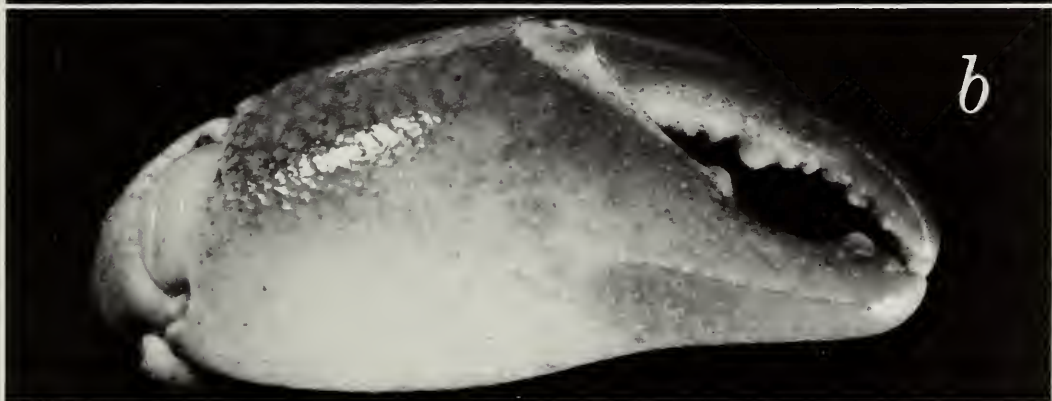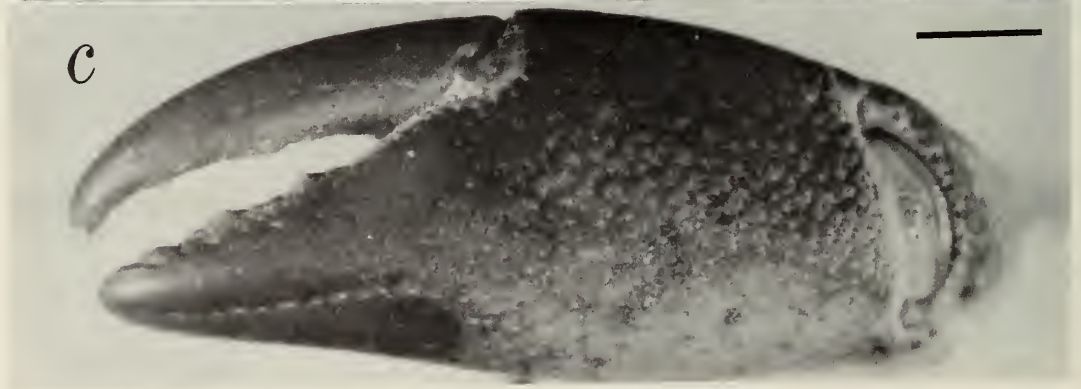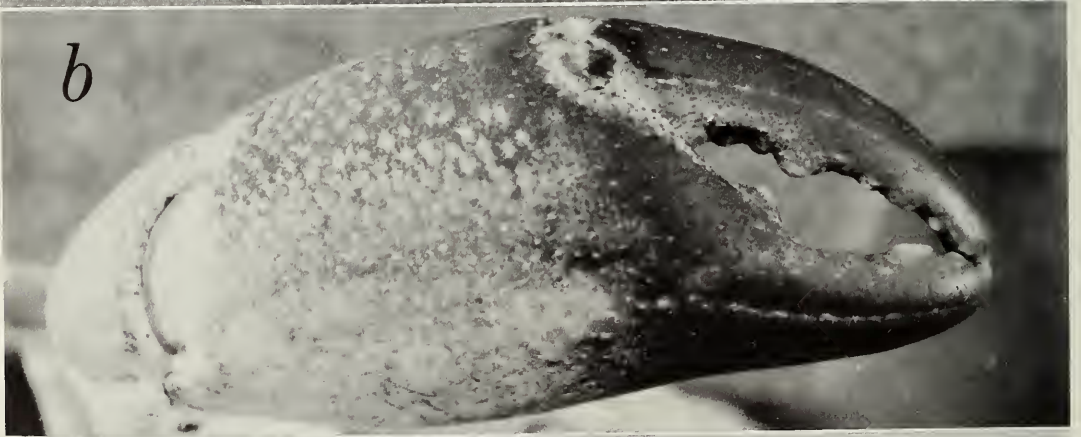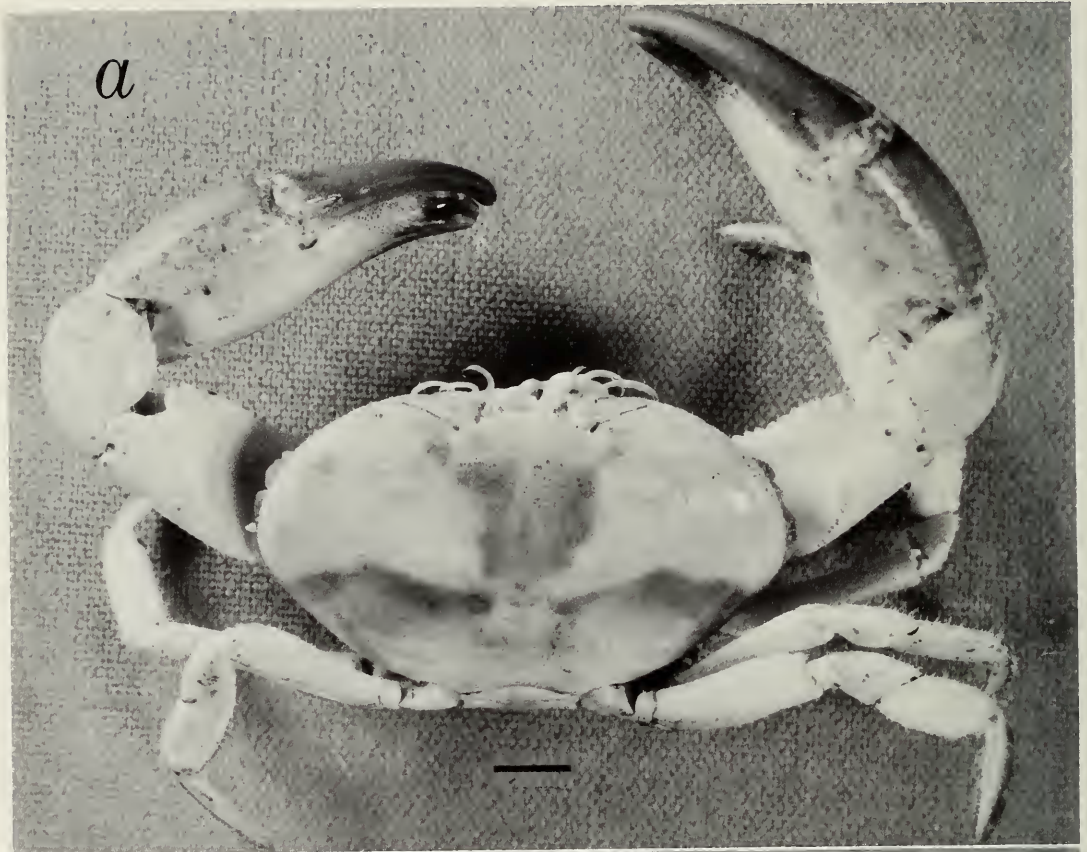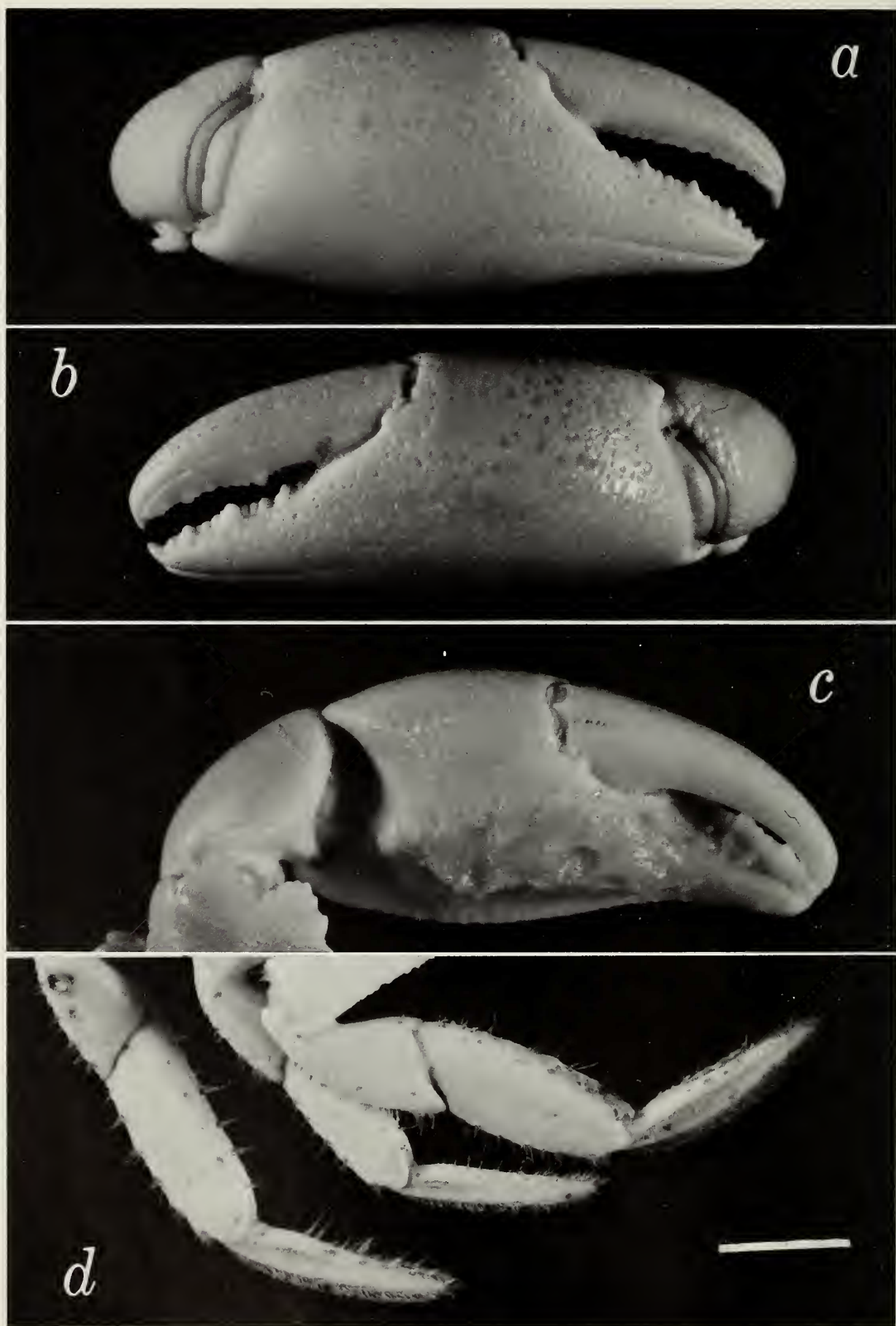
Fig. 4.   *Bythograea thermydron*. Female allotype: **a,** Right, **b,** Left chelae in external view; **c,** Left chela, internal view. **d,** Female paratype (USNM 172832), distal articles of third–fifth legs. Scale = 1 cm.

broadened proximally where hidden under front but distally narrowing at base of compressed but slightly swollen, fusiform tip; unpigmented cornea laterally oriented, smooth, exposed beyond supraorbital margin, fringed with soft hairs laterally.

Epistome projecting well beyond front, lying nearly in frontal plane, its anterior margin cut into 6 unequal lobes variably darkened at edge, submedian lobes separated by narrow deep notch, intermediate lobes less advanced, laterals large, irregular, and folded slightly ventrad in males.

Antennules folding transversely, stouter than antennae, large bulbous basal articles contiguous, concealed beneath front, interantennular septum represented by minute remnant at upper and lower edge of antennular fossa; slender penultimate and terminal articles of peduncle nearly equal in length, former slightly hollowed laterally, latter slightly longer and more slender. Flagella short; mesial 8-segmented ramus slender; slightly shorter lateral ramus curved, multisegmented, thick at base but tapering to point, its dense mesial brush of long sensory setae exceeding chord of curve.

Antennal insertion below eyestalk; peduncle mesial to eyestalk, extending obliquely nearly to margin of cornea in situ; fixed article broad but short; first free article slender, ca. 1.8 times length of second article; latter broadened distally; terminal article short, its diameter only slightly greater than that of flagellar base; flagellar length ½ to slightly exceeding frontal width.

Afferent branchial openings above base of chelipeds broad.

Mouth field divergent anteriorly, its frame broadest posteriorly and somewhat swollen and granular at anterolateral corners, maximal inside anterior width about 1.25–1.4 times minimal inside posterior width. Third maxillipeds filling mouth field except for narrow gap of nearly uniform width between ischia of endognaths and rather irregular gap anteriorly between meri-carpi of endognaths and epistome; exognaths overlapping sides of mouth frame. Endognaths with exposed surface of ischium nearly smooth; elongate polygonal in outline but primarily rectangular, greatest (distal) width 1.2–1.8 times narrowed part ca. ⅓ length from base; mesial margin straight, toothless, bearing many stiff straight setae, submarginal zone somewhat thickened and flanked laterally by shallow longitudinal groove; anterior margin nearly perpendicular to mesial margin except for anteriorly projecting truncate lobe at inner corner, beaded with tiny, often darkened granules; lateral margin concave; posteromesial margin obliquely convex; basi-ischial suture line visible posterolaterally. Merus slightly narrower than ischium, tilted dorsally from insertion in flexed position; ventral surface punctate, occasionally with scattered, obsolescent granules having tips directed anteromesially (often darkened and in irregular oblique rows); irregularly quadrate perimeter flanked by submarginal thickened zone and groove similar to mesial counterpart on ischium except on straight proximal side, anterolateral angle broadly rounded, anteromesial angle at insertion of palp
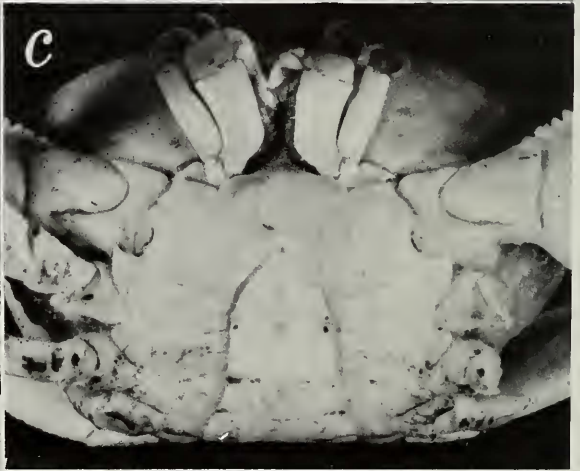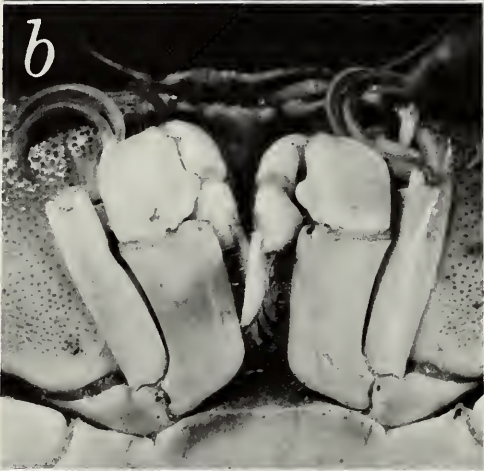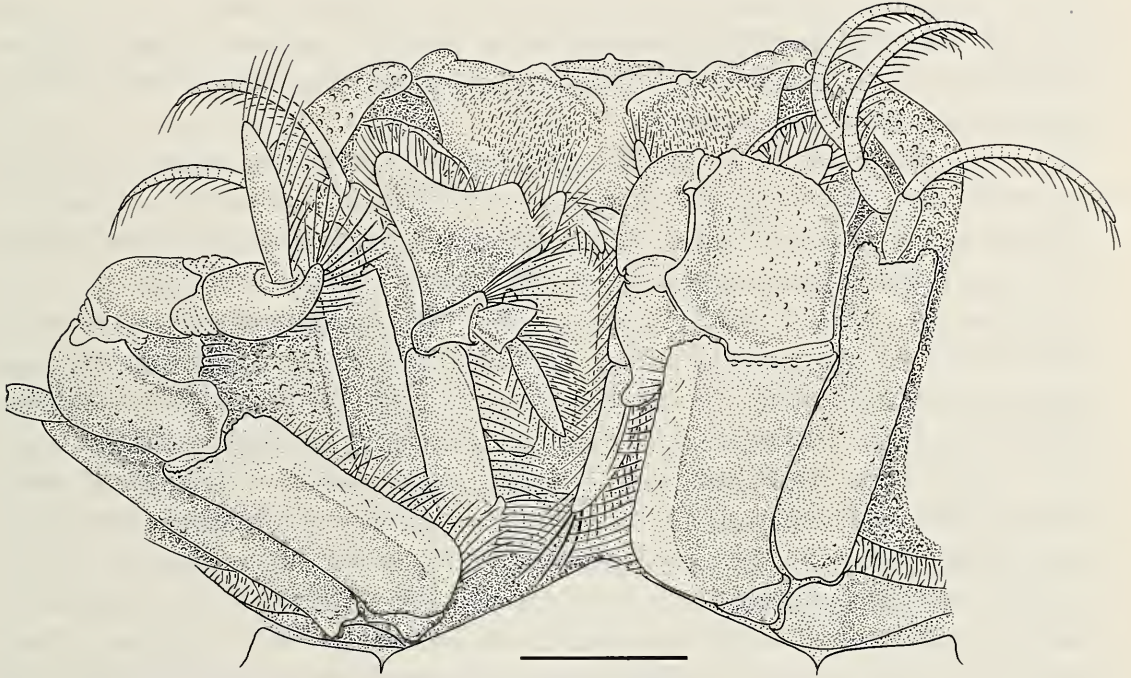
Fig. 6. *Bythograea thermydron*. Female allotype. Mouth field region showing third maxillipeds, endognath of right second and first maxillipeds in situ with overlying third maxilliped turned aside, outline of right mandible, and pubescent mesial part of endostome. Scale = 5 mm.

shorter and oblique; mesial margin doubled for reception of palp, its ventral (exposed) side almost straight distally but lobed at level of carpo-propodal articulation, posteromesial corner fitted to projecting lobe of ischium, dorsal (hidden) side produced behind carpus, its margin setose. Palp large, dactyl reaching posteriorly about ½–⅔ length mesial margin of ischium. Carpus expanded distally, narrowed proximally, bent nearly at right angle near insertion and crimped inside angle; dense tuft of setae on disto-oral surface. Propodus wider than carpus, longer than broad; asymmetrically ovate in ventral view; distal (longest) margin convex, densely beset with rows of strong serrated setae, longest distally; distal tuft of such setae on dorsal surface. Dactyl half-ensiform (knife blade-like), deeply inserted in mesial and distal sides of propodus in flexed position, mesial edge (back of knife blade) straight, gently curved lateral margin (knife edge) setose like propodus. Exognath narrow, not extending to full length of merus; ventral

←

Fig. 5. *Bythograea thermydron*. Male paratype USNM 172832: **a,** Frontal region; **b,** Third maxillipeds; **c,** Sternum with abdomen in situ. **d,** Female paratype (USNM 172832) with abdomen unfolded showing sternum, female openings, pleopods and small egg mass.

surface with few granules as on endognath; slightly curved mesially to fit closely lateral side endognathal ischium, with dorsomesial flange (widest distally) fitting beneath latter; palp conspicuous, flagellum densely beset with setae in hollow of curve.

First maxilliped with lacinia of endopod broad, its somewhat concave to slightly sinuous distal edge advanced anterolaterally in rounded corner; anteromesial corner less advanced and separated by conspicuous notch from still less advanced moderately ovate mesial lobe.

Endostome large, divided by low median sagittal ridge bifurcated somewhat anteriorly and merging into projecting endostome; each half of palate shallowly concave, mesial ⅓ variably covered with velvety pubescence limited laterally by low longitudinal ridge curving from near base of large mandibular palp to lateral epistomial lobe, lateral smooth ⅔ receiving broad efferent branchial channels; each palatal ridge most prominent posteriorly and bearing single row of very fine, close-set, transverse rugae.

Chelipeds heavy, unequal; surface slightly and variably rugose (pebbled), tending to slight imbrication here and there with transverse pattern on meri, punctate; chelae externally inflated, lower margin of palm arched downward and with rather pronounced keel merging into fixed finger, inner surface with concavity above keel limited by swollen central surface of palm most pronounced proximally (rather sharply so in females), that surface glabrous in males but bearing central patch of dense plumose hairs in females. Males with fixed fingers rather short, stout, distal half of lower margin almost straight but abruptly curved upward at narrowly spooned tip, a mesiolateral, longitudinal impressed line running from base of terminal tooth to distal part of palm; dactyls more slender, rather long, arching down to close in distal notch of spooned tip of fixed finger. Major chela of males often with strongest tooth (low and essentially tripartite) on each finger almost opposed at about ⅓ length; dactyl with 2 low teeth proximally and 3 or more low irregularly spaced and shaped teeth distally, but cutting edge sometimes essentially as minor chela; fixed finger with diastema between major tooth and 3-toothed (low) area on raised external edge of spoon near tip, inner edge of spoon shorter and less elevated. Minor chela with fingers more uniformly toothed, but teeth low and entire cutting edge sometimes nearly toothless; spoon essentially as on major chela. Chelae of female with fingers not gaping; tooth rows continuous and fairly regular; that of major fixed finger continuous, 12 teeth, 4 larger ones including tip, 2 smaller teeth in intermediate spaces, largest central tooth with minute flanking cusp to each side forming triad; minor fixed finger with 14 smaller, more uniform teeth. Dactyls each with complete tooth row, those of major somewhat larger and more irregular.

Carpus with internal margin rounded in outline, granular. Merus broadened mesially into cristate flange slightly rounded in distal extension falling

short of mero-carpal condyle, strong granules in single line along margin; outer surface rounded. Fused basis-ischium articulated with merus. Coxa broadly emarginate ventrally for insertion of basis-ischium, cup thus formed projected anteriorly into stout triangular spine and posteriorly into longer, stout spine with subterminal notch and suture.

Walking legs rather long, flattened, length decreasing slightly from first to last; conspicuous darkened setae in 3 rows of rather sparse tufts on extensor surface of carpus and propodus, on flexor surface of propodus and more densely spaced on dactyl, also scattered tufts laterally on these articles, densest tract of setae on extensor surface of dactyl. Meri with upper margins granular, posterior sides of first 2 pairs slightly rugose, that of last 2 pairs less granular; lower margins granular, somewhat cristate, anterior lower margin present throughout length but posterior lower margin obsolescent proximally. Carpi with posterior, shallow, longitudinal groove paralleling dorsal margin. Mean maximum length of propodi about 2.5–3.0 times mean maximum width (of last leg relatively shortest and broadest), that of dactyls about 4.5–5.5 times width. Dactyls slightly shorter than propodi, narrowly lanceolate, shallowly grooved longitudinally on flattened anterior and posterior sides, tip stout, corneous.

Sternum broadest between first and second legs, narrower posteriorly.

Male abdomen composed of 6 free segments gradually increasing in length distally, 4 and 5 partly fused; first 2 and part of 3 visible in dorsal view; 1 arched to fit contour of adjacent carapace, 2 and 3 filling all of space between fifth legs, 3 broadest, 4 nearly as broad, 5 narrowing, 6 narrowest with almost parallel sides, its greatest width 1.6 times its median length. Telson broadly triangular, width 1.37–1.4 times length; no sternal groove anterior to tip; furry covering on sternum beneath; entire abdominal groove deep.

Abdomen of mature female nearly covering sternum, ovate in outline and densely fringed with hairs, fully segmented; narrowest first segment arched dorsally to fit contour of adjacent carapace, segments 2–5 of about equal length, 6 longest, 2–3 broadening abruptly to greatest width reached in 4–6; telson nearly as broad as 6, broadly arched distally. Segments 2–5 bearing large, well developed biramous pleopods, outer curved branch lying near edge of abdomen heavily plumed with soft hairs laterally and mesially, inner branch more sparsely equipped with ovigerous setae and jointed.

Sternum beyond outline of abdominal segments bearing dense fringe of fine plumose hairs, tract extending to limited extent on coxae of legs 1–4, chiefly 2 and 3. Female openings large, oval membranous area (1.88 × 3.5 mm in ♀ 172831); 1.75 × 3.0 mm in ♀ 172832) surrounding central, transverse, lunate slit.

Eggs spherical to slightly oval (mean of 5 = .77 × .83 mm short and long axes).

Male openings coxal. First pleopods stout, dextrally twisted, S-curved,
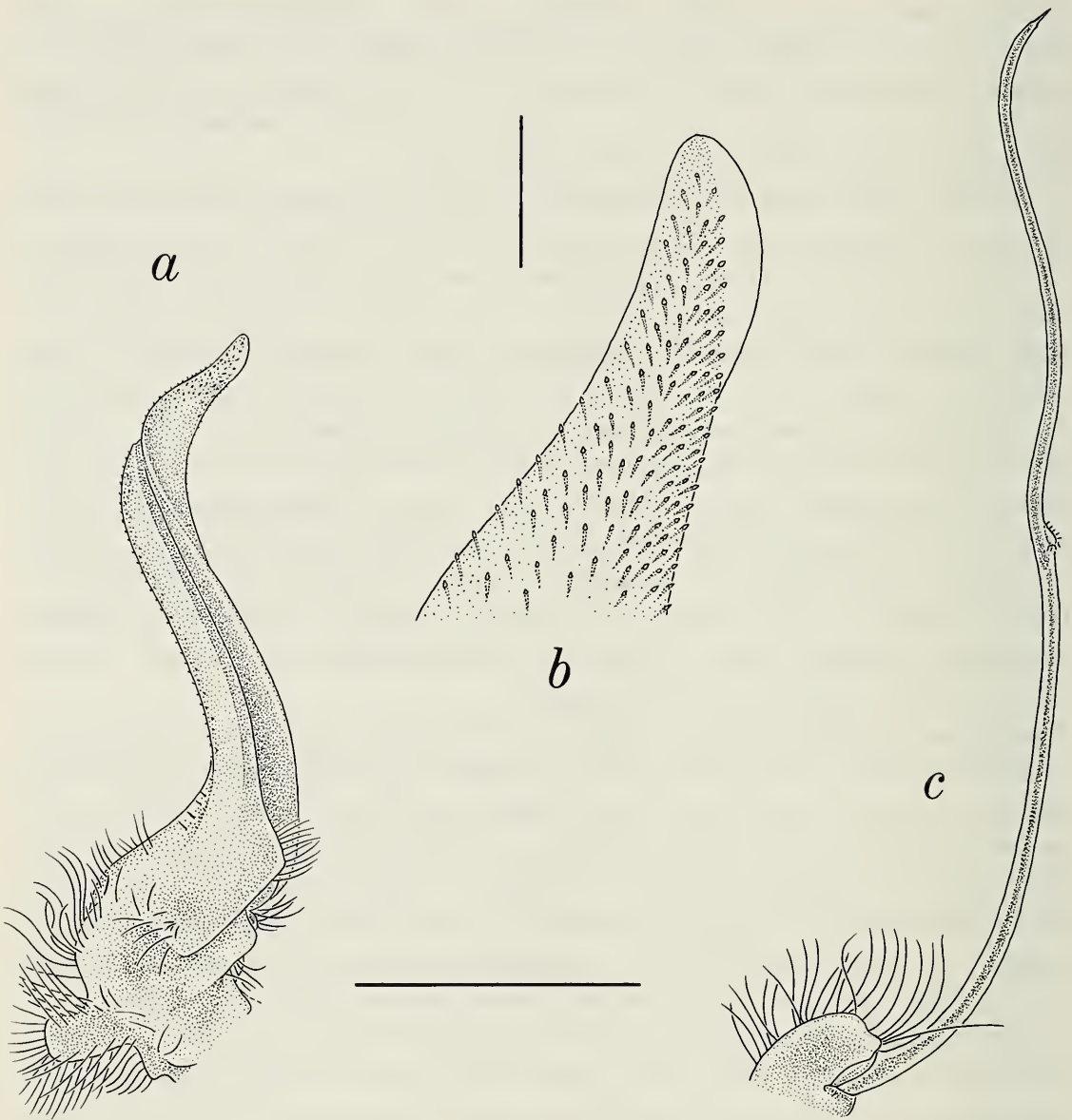
Fig. 7. *Bythograea thermydron*. Male paratype USNM 172832: **a,** First, **c,** Second pleopods in ventral (abdominal) view; **b,** Tip of first pleopod. Scales: **a, c** = 5 mm; **b** = 0.5 mm.

well separated, darkened somewhat distally and drawn to acute but slightly spatulate tip reaching almost to darkened locking tubercles on sternite V, shaft angled in X-section and grooved mesioventrally in proximal half for lodgment of second pleopod; multitude of exceedingly minute retrogressive spinules in lateral and anterolateral tract, and less densely distributed to each side of this and around tip; meso-abdominal aspect nearly smooth, a setose angle over second pleopod near base. Second pleopods slender, long, crossed, exceeding first pleopods and extending almost to tip of telson lodged halfway along sternite IV; distal half amber-translucent and whiplike.

Fig. 8. Carapace length-width relationships of mature *Bythograea thermydron*. ♂, N = 36; ♀, N = 100.

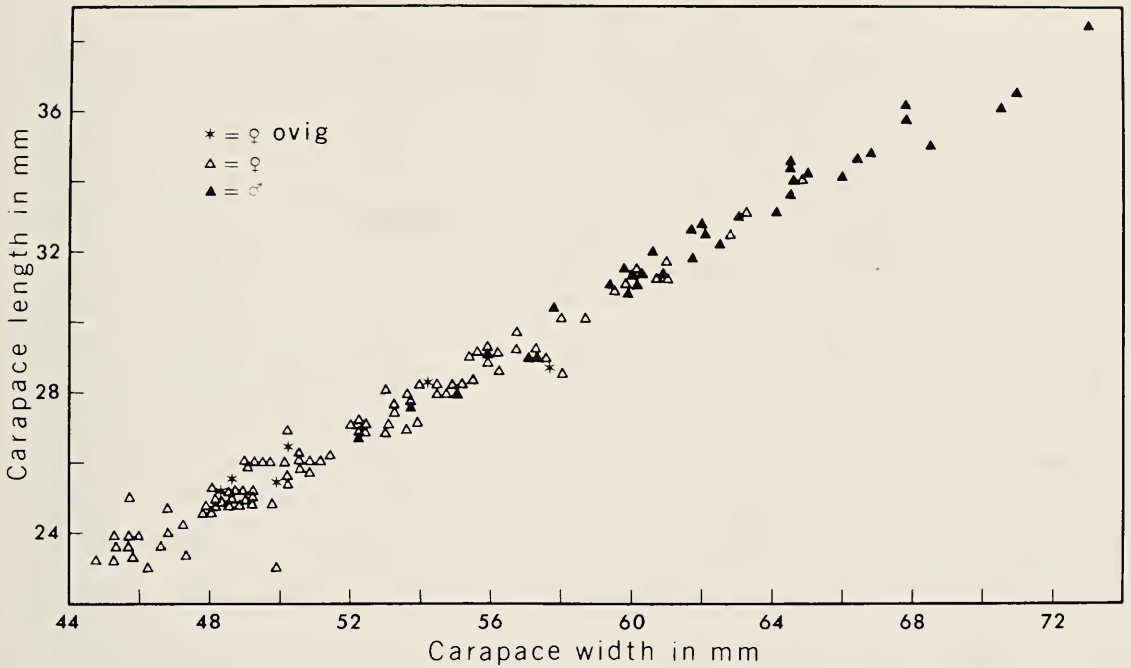*Measurements in mm.*—Holotype ♂ (USNM 172830), allotype ♀ (USNM 172831), R right, L left.

	Length cara- pace	Width cara- pace	Depth thorax	Orbito- frontal width	Propodus lower margin	Dactyl length	Palm height	Palm thickness
H ♂	33.1	59.4	21.0	15.3	R 48.3	R 28.5	R 23.5	R 16.0
					L 45.6	L 25.7	L 21.8	L 15.2
A ♀	30.7	57.7	18.5	14.3	R 38.8	R 22.5	R 18.8	R 12.2
					L 38.7	L 22.5	L 18.8	L 13.0

Selected measurements of material studied, including the above type-specimens are shown in Figs. 8 and 9. All specimens are mature. Openings to the traps were size selective. The complete range of sizes is not represented in this sample. Both smaller and larger crabs were observed from the submarine during the third set of dives in November–December 1979 (D. M. Cohen and J. F. Grassle, personal communication).

Carapace length-width relationships of males and females fall in a narrow band that describes a straight line (Fig. 8), the range limits for the two sexes covering spans of almost equal length, but males on the whole attain larger sizes than females. Ovigerous females are scattered along the female size range but do not occur at the extremes of this sample.

Cheliped sizes also reflect sex differences, and, moreover, their bilateral
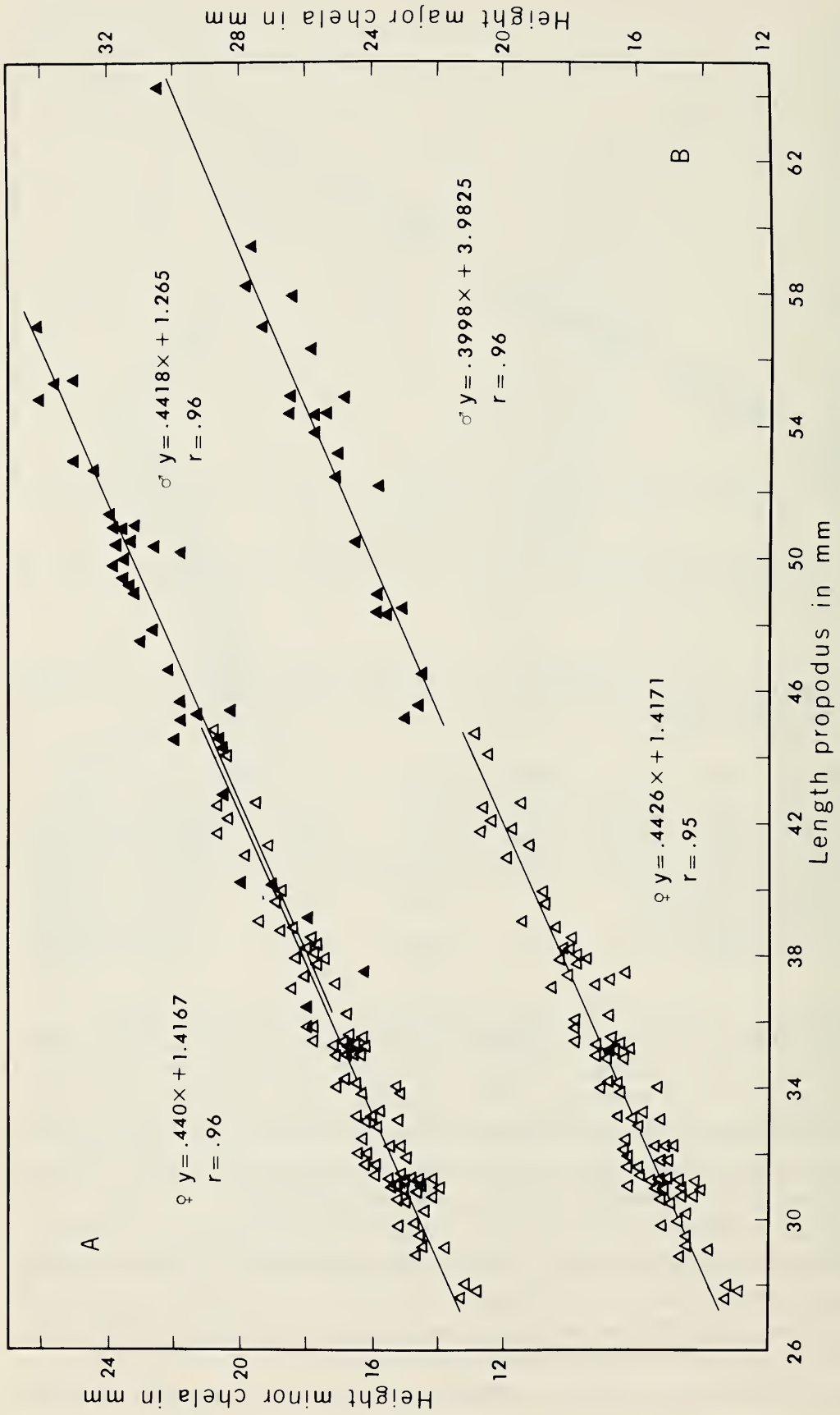
Fig. 9. Mature *Bythograea thermydron*. A. Length-height relationships of minor chelae (length lower margin of propodus–maximum height of palm) regardless of size, excluding those obviously distorted by injury. ♂, N = 35; ♀, N = 84. B. Same for major chelae (either the larger of two chelae on a specimen or an undoubted major where minor was missing). ♂, N = 23; ♀, N = 84.

asymmetry in form (major–minor) can be altered by loss and reversals in form that accompany regeneration. Although there appear to be intermediate forms associated with cheliped regeneration and reversal, there is always some difference in the size of these two limbs on an individual. These differences can be represented by plotting the straight-line length of the lower propodal margin against maximum height of palm for each chela measured. For this sample, the scatters of points describe straight line relationships (Fig. 9) for both major and minor chelae. Range limits for the minor chela of males and females overlap, those for males covering a greater span at larger sizes than for females (A), but the scatter of points for both fall on essentially a common line. The plot for the major chela differs in two easily observable ways; the female hand is both shorter and less elevated than that of the male, there being no overlap in length for the two sexes in this sample. The elevated male palm height follows a common trend in the Brachyura for sexually mature males to possess noticeably enlarged crushers.

Color in life.—Dominant color white with chelae dark to quite black, especially on fingers. Ova in female's bodies reddish or pronounced pink; hepatic gland grayish. Crabs from "The Rose Garden" white and not worn; those from "The Mussel Bed" quite stained, worn, and with quite black chelae, the mussel beds themselves being somewhat darkened (J. J. Childress, personal communication).

Color in preservation.—Predominantly whitish or moderately greenish but variable; latter color (which possibly results from ruptured internal organs) on subdivisions of gastric, hepatic, subhepatic, suborbital parts of pterygostomian and subbranchial regions, and solid, variable or mottled on branchial, cardiac or intestinal regions in some specimens, often along epibranchial line, and with almost symmetrical greenish spots on lighter green background in still other specimens. Fingers with outer aspect slate colored, in males often solidly so, but females often with darker color below impressed lateral line of fixed finger than immediately above it; color extending almost solidly along upper margin of palm and variably from below tooth row and base of fixed finger onto outer surface of palm, often reticulated and darker along upper half, especially in males, and grading into lighter background of white sometimes tinged with pink on relatively uncolored lower proximal quadrant. Inner surface of fingers less solidly colored. Males with sooty to dusky speckles dusted on palm; carpus lightly dusted with continuation of external speckles on outer surface of palm, suggestion of same externally on inner corner of merus as well as a few such areas (sometimes faded) on walking legs. Some females entirely white.

Of 36 males and 99 females, all males had variable dark coloration as above; many females were similar but usually lighter colored, the darkened areas of the chelae varying from shadowy light or pinkish gray to tannish

gray to slate color. Color pattern and intensity varied greatly. Lighter colored, "cleaner" individuals appeared to be more freshly molted, having sharply granular or punctate though completely hard exoskeletons, than the darker more worn individuals. Degree of wear, mainly in males, appears to be associated with increasing number and density of the irregular sooty or dusky spots, blotches and trace marks, suggesting that these are at least in part induced by friction, especially on prominences where oblique marks give evidence of abrasion.

Name.—The specific name from the Greek "thermydron," hot spring, is a noun in apposition, referring to discovery of the species in association with the thermal vents.

Megalopae and Juveniles
Figs. 10–11

Clumps of mussels taken from the bottom (discussed and figured, Corliss and Ballard, 1977; Corliss et al., 1979) sheltered a few specimens best characterized as "crablike megalopae," and early crab stages. One juvenile was found in association with vestimentiferan tubes. None of these were taken in the traps. J. F. Grassle saw one megalopa swim past a viewing port of the *Alvin* on a November–December 1979 dive.

Material.—Two megalopae, USNM 173501, Galapagos Rift, Garden of Eden, 25 January 1979, 0°47.69′N, 86°07.74′W, 2482 m, *Alvin* Dive 884. Five megalopae + 1 megalopal exuvium and 6 early crab stages, USNM 180065, Rose Garden, 30 November 1979, 0°48.25′N, 86°13.48′W, 2460 m, *Alvin* Dive 983 (mussel washings). One juvenile ♂, USNM 180066, Rose Garden, 7 December 1979, 2458 m, *Alvin* Dive 990 (found with vestimentiferan tubes).

Megalopa description.—The megalopae have megalopal eyes and abdominal characters but resemble early crab stages in general body shape.

Integument clothed with numerous, conspicuous, plumose hairs trapping a flocculent material. Carapace crablike, elliptical, broader than long, mostly smooth dorsally, regions somewhat defined. Anterolateral margins arched, notched between hepatic region and remaining margin; edge running to corneous outer orbital tooth in smaller specimens but a little below this tooth in larger specimens; tiny, corneous, forward trending spines on hepatic margin and surface dorsally, becoming smaller and reduced to granules posteriorly on anterolateral margin and disappearing at lateral angle; slight offset behind lateral angle at juncture of epibranchial line with convex posterlateral margin; short posterior margin concave.

Eyestalks thick and short; cornea globular, swollen and facetted, amber in preservation, not black; folding laterally into cupped orbits with both upper and lower margin complete, 1 or 2 low spines on upper edge.
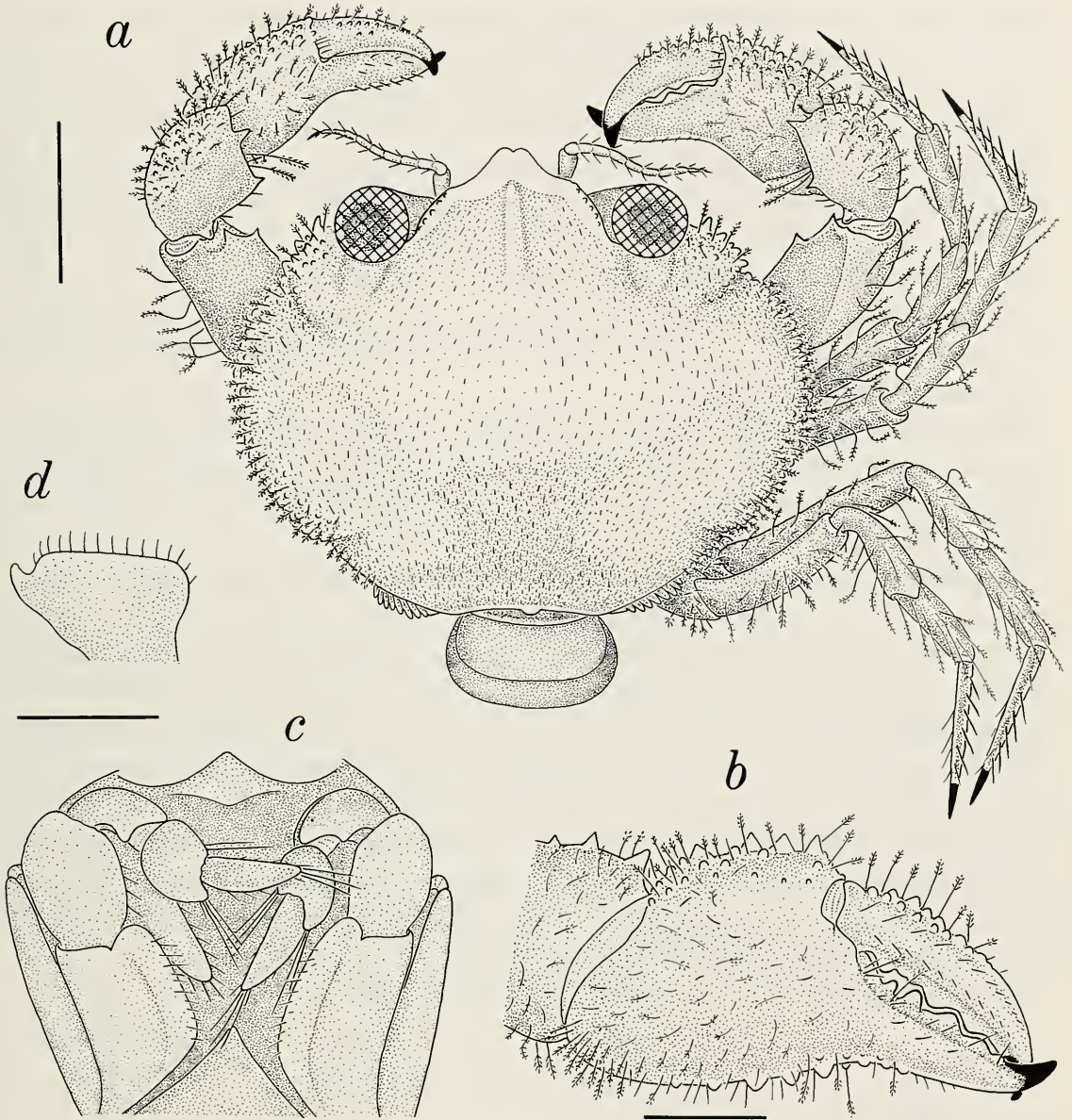
Fig. 10. Larger megalopa from mussel clumps. **a,** Dorsal view, walking legs of left side not shown; **b,** Right chela, external view; **c,** Mouth field showing third maxillipeds with palp of right turned aside, endognath of second maxilliped beneath; **d,** Distal part of left first maxilliped, showing mesial lobe on lacinia. Scales: **a** = 2 mm; **b–d** = 1 mm.

Rostrum bilobed in dorsal view, concave between submedian and inner orbital lobes (latter covering more of eyestalks in larger than in smaller specimens), rather obtuse triangular tip deflexed and extended well below bases of antennal peduncles (somewhat shorter in smaller specimens).

Interantennular septum incomplete.

Antennal flagellum reaching about ⅓ its length beyond outer orbital tooth.

Chelipeds well formed, strong, essentially equal; palms inflated, conspic-

uous but scattered, rounded, corneous granules on external surface contin-
ued both on carpus and proximodorsal edge of dactyl, largest and most
dense dorsally (more prominent on smaller specimens); fingers moderately
slender, deflexed, irregularly but completely armed with closely fitting teeth,
narrowest proximally, broadest in distal half, tips subacute, crossing (dactyl
inside) and darkened; merus with short spine at anteromesial angle; carpus
with similar spine at middle of inner margin and another between it and
articulation with propodus; palms smooth internally.

Walking legs shorter than chelipeds but fairly long, slender, and slightly
flattened distally, coxal spines absent; dactyls acute, that of fifth leg about
1.5 times length of propodus.

Mouth field with sides slightly divergent anteriorly; outline of third max-
illipeds resembling that of adult crabs described above but merus relatively
longer. First maxilliped with lacinia of endognath broadened distally and
bearing mesial lobe.

Sternum longer than broad, larger specimen with sternites I–IV almost
equilaterally triangular in outline and nearly equal in area to V–VIII; deeply
and broadly grooved for reception of abdomen. Abdomen not fixed beneath
thorax, 6-segmented, first segment very short, anterior of remaining seg-
ments longest; posterolateral spines absent from sixth segment. Four pairs
of biramous pleopods with exopods diminishing in length from anterior long-
est to posterior shortest, each on larger specimens bearing about 36 very
long setae, endopods short, slender, tipped with retinacula coupling with
member of opposite side; uropods flanking sixth segment short and unira-
mous, those of smaller specimens bearing 21–22 and of larger specimens
26–28 setae; telson broadly convex distally.

Measurements in mm.—15 specimens examined.

USNM	Length carapace	Width carapace	Frontoorbital distance
173501 Megalopae	4.3	5.3	3.8
	6.1	7.6	5.1
180065 Megalopae	3.8	5.3	3.4
	4.3	5.5	4.0
	4.4	5.8	4.1
	6.3	8.0	5.1
	6.3	8.1	5.4
Megalopa exuvium, width in 8-mm class			
Early crab stages	4.1	6.0	
	4.3	6.3	
	4.3	6.6	
	4.3	6.8	
	4.4	6.6	
	4.5	6.8	
180066 Juvenile ♂	12.5	21.1	
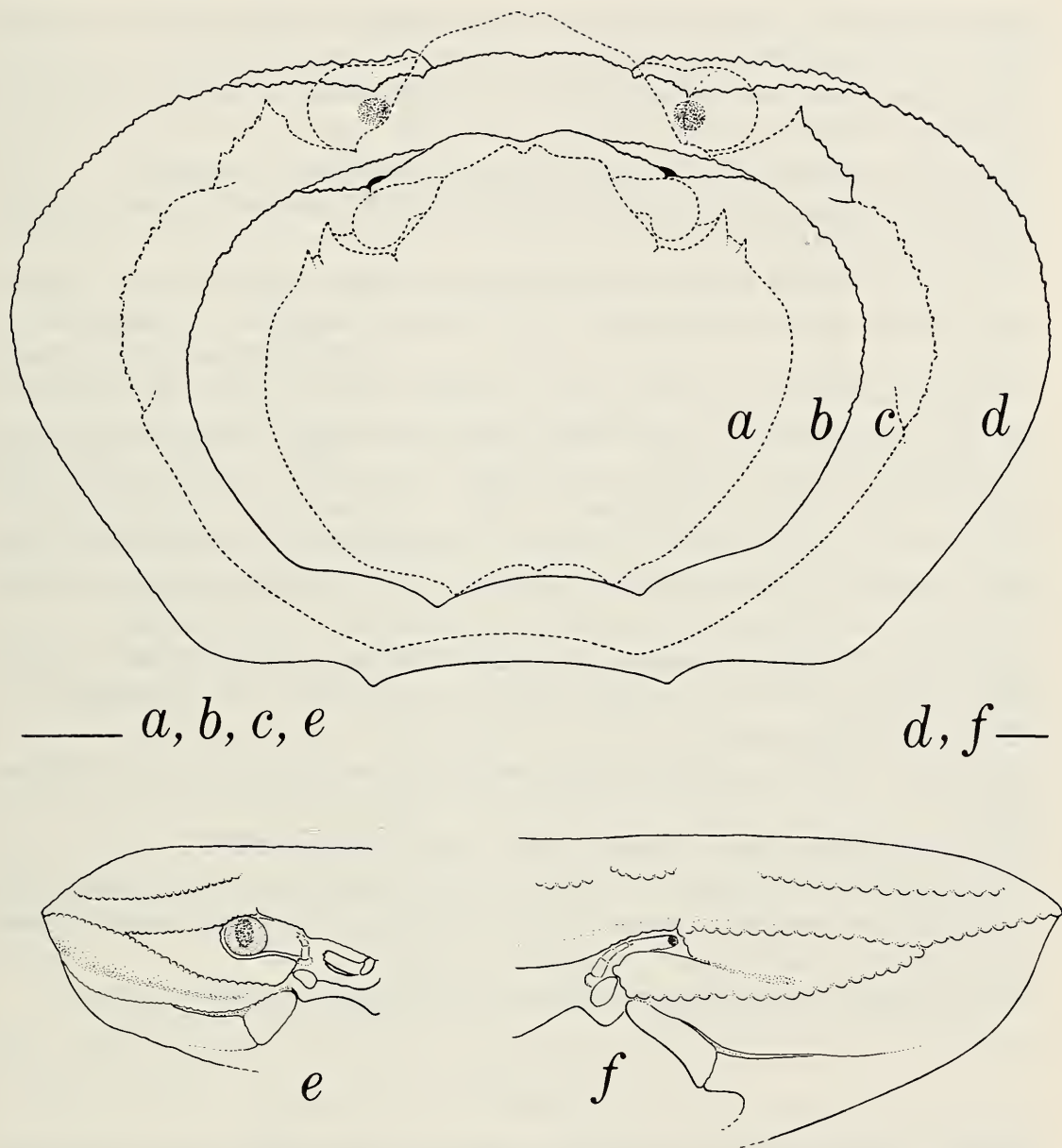
Fig. 11. **a–b,** Outlines of carapace, megalopae and juveniles in dorsal view, see length measurements: **a–c,** USNM 180065, 3.8, 6.3, and 4.5-mm specimens; **d,** USNM 180066, 12.5-mm specimen; **e,** Orbital area of 4.5-mm specimen in frontal view, antenna deleted; **f,** same, 12.5-mm specimen. Scales: **a–c, e** and **d, f** = 1 mm.

Early crab stage.—Adult in general facies but transitional between me-galopae and later stages as follows (Fig. 11):

Carapace often nearly featureless dorsally except for indication of most prominent granular lines on surfaces and margins. Front deflexed; shallow median concavity visible in dorsal view; submarginal row of granules slight-ly interrupted medially. Orbits slightly arched over eyes and open laterally but bounded there by line of granules along supraorbital margin and along

edge of suborbital plate converging at anterolateral margin; suborbital plate hidden in dorsal view.

Eyestalks thick, extending laterally; corneal surfaces amber colored but with facets obsolete.

Epistome hidden under front but its essential features present.

Third maxilliped with sides of ischium nearly parallel; merus approximately same width.

Chelipeds similar in size but already somewhat asymmetrical. Chelae, carpi, and meri minutely rugose on all surfaces, tendency on palms to arrangement in alternate rough and smooth horizontal bands on outer surface and raised granular or rugose rows dorsally and ventrally, in transverse rows on meri laterally. Fingers with longitudinal ridges bearing many close-set, distally directed, minute, acute teeth on external surfaces; tips light colored; tooth rows on prehensile edges well formed, in incipient cutter-crusher form, though sharp and more completely developed on fixed finger than on dactyl. Carpus with tiny internal spine and longitudinal, shallow dorsal groove. Merus with mesiodistal spine at end of distal crest.

Abdomen broadest basally, tapering distally, intersegmental sutures slightly narrowed, that between 5–6 narrowest. Telson convex distally.

Pilose patches absent.

Juvenile ♂.—Essentially as adult but transitional from earlier stages as follows:

Eyes reduced, almost hidden, cornea slightly darkened.

Frontal, orbital and outer orbital margin finely milled; anterolateral margin bearing numerous acute, close-set, exceedingly fine, foreward trending teeth diminishing to obsolescence on posterior margin.

Pilose patches on subbranchial areas and chelae as in older males.

Remarks

Adults.—*Bythograea thermydron* has an appearance that immediately suggests the cancroid crabs, but is so obviously modified that no known family of crabs has a suite of characters that includes it (Table 1). The bythograeid family characters are suggestive of portunoid or xanthoid affinities; indeed only the Portunidae have a "portunid lobe" on the endognath of the first maxilliped. Balss's (1957) keys place *B. thermydron* in the Tribe Brachygnatha, Superfamily Brachyrhyncha, between the Families Portunidae and Potamidae s. l. (emend. Glaessner, 1969). In Glaessner's (1969) system, *B. thermydron* could be placed in the Section Brachyrhyncha, Superfamily Portunoidea; the front in that superfamily is defined as "narrow or wide, dentate or lobed," and hence broadly interpreted could accommodate it. Also, the flattened but not leaflike distal articles of the fifth legs resemble those of *Carcinus maenas* (Linnaeus) (Carcininae), *Catoptrus inaequalis*

(Rathbun) (Catoptrinae), and *Caphyra rotundifrons* (A. Milne Edwards) (Caphrinae), and the broad rounded adult female abdomen with wide telson resembles that of *Caphyra laevis* (A. Milne Edwards) (Stephenson, 1972; Stephenson and Campbell, 1960). The chelae, however, are not ridged except for the mesioventral palmar keel somewhat resembling that of *Ovalipes* (Polybiinae). The produced anterolateral margin, granular and lacking teeth or lobes, is reminiscent of some freshwater Potamidae s. l., but in other respects this similarity must be regarded as superficial (Table 1).

Following are additional considerations that make the systematic placement of this crab difficult:

The predominantly smooth inflated chelae with spooned fixed finger are more xanthoid than portunoid. These appendages undoubtedly are adapted for feeding, for the crabs were caught in baited traps, indicating ability to scavenge. Moreover, patches of dense plumose hairs on the submarginal and subbranchial areas of the carapace, bases of legs, endostome mesial to the palatal ridge, and on the inside of female palms and sternum at perimeter of the abdomen may be at least partly for entrapment of finely particulate food, recalling similar patches of hair among the Goneplacidae, *Euryplax nitida* Stimpson or *Frevillea hirsuta* (Borradaile); for example (Guinot, 1969). C-CD video tapes from the Galapagos II Expedition show the crabs moving backward over the large vestimentiferan (pogonophoran) tubes, apparently sweeping fine material from the tube surfaces toward the mouth by alternate movements of the third maxillipeds. Also, females may preen egg masses with aid of the internal hairs on the chelae. Tufted bands of setae on the walking legs suggest great tactile sensitivity (activity viewed on C-CD video tapes).

Capacious branchial areas with large afferent and efferent branchial openings suggest adaptation to an environment that can be low in dissolved oxygen (Corliss et al., 1979).

The male first pleopods have the same general curvature as in many portunids with short pleopods, but they are much stouter; the long whiplike second pleopods are unlike any in the Portunidae (usually short or whiplike) but resemble those of xanthids such as *Menippe mercenaria* (Say) (Williams, 1965) and platyxanthids (Guinot, 1968; 1978). Females have correspondingly enlarged gonoducts. All females taken in the samples are adult, therefore no data are available on abdomen shape in juvenile females which might give clues indicating family affiliations.

The greatly modified adult orbits result from combined reduction of eyestalks and lateral expansion of the carapace, the supraocular border *per se* becoming relatively shortened, but the narrow granular, outer orbital area lying between the extended anterolateral margin and dorsal line of granules lateral to the supraorbital margin becoming larger during development. Neither this complex nor the projecting somewhat deflexed suborbital plates

Table 1.—Comparison of predominant adult characters in five closely allied families of Brachyura; there are many exceptions.

Character	Portunidae	Bythograeidae	Potamidae s. l.	Xanthidae	Goneplacidae
				(Not sharply distinguished)	
Carapace	Flat, moderately transverse, usu. widest at last marginal spine	Flat, transversely oval	Rectangular, oval or rounded	Broader than long, oval, hexagonal, subrectangular, rarely circular	Trapezoidal to rectangular
Anterolateral margin	Variably convex, usually toothed	Convex, not toothed	Convex, toothed or not	Usually toothed or lobed	Usually toothed or lobed
Branchial region	Normal	Expanded	Expanded	Normal	Normal
Front	Horizontal, toothed or lobed	Nearly horizontal, bilobed	Mostly broad, straight or bilobed, deflexed	Broad, often notched, occ. toothed, never produced as rostrum	Transverse, slightly notched, occ. deflexed
Orbits	Bipartite, large	Incomplete	Bipartite, large	Bipartite, normal	Not bipartite, normal, reduced, or large
Eyestalks	Moderately large or elongate	Reduced, blind	Moderate to large	Normal	Small to large, occ. elongate
Antennules fold	Transversely or obliquely	Transversely	Transversely	Transversely or slightly obliquely	Transversely
Interantennular septum	Present	Absent	Present	Present	Present
Chelae	Palm ridged; fingers extended	Palm inflated, ventrally keeled; fingers mod. extended, tip of fixed spooned	Palm usually smooth; fingers extended	Palm smooth, toothed, spined or tuberculate; fingers short, tip of fixed occ. spooned	Palm usually smooth, fingers usually deflexed

Table 1.—Continued.

Character	Portunidae	Bythograeidae	Potamidae s. l.	Xanthidae	Goneplacidae
				(Not sharply distinguished)	
Mouth frame	Sides nearly parallel; mxp. often overlapping ant. margin	Sides divergent; mxp. not overlapping ant. margin	Sides nearly parallel; mxp. not overlapping ant. margin	Sides nearly parallel; mxp. not overlapping ant. margin	Sides divergent; mxp. not overlapping ant. margin
Mxp 1 endognath	Usually lobed	Lobed	Not lobed	Lobe extremely rare	Not lobed
P 5 flattening	Marked; dactyl leaf-shaped usually	Marked; dactyl narrowly lanceolate	Moderate; dactyl ambulatory, often spined	Moderate; dactyl rarely leaf-shaped	Moderate; dactyl ambulatory
♂ gonoducts	Coxal	Coxal	Coxal	Coxal	Sternal or coxal with sternal grooves

and associated projecting epistome have an exact counterpart in the Brachyura. Blindness is a common reductive adapatation in deep-sea animals. Although there are no known blind portunids, a rough parallel to this orbital plate development might be found in *Euphylax dovii* Stimpson or *Podophthalmus vigil* (Weber), portunids (Podophthalminae) with greatly elongated eyestalks which fold into transverse troughlike orbits open laterally for the reception of an expanded cornea.

Narrowing of the interantennular septum is carried to an extreme, that structure being indicated only by minute remnants in the adult and for all practical purposes is absent.

Megalopae and Juveniles.—Characters of the megalopae can be compared to those of the portunid subfamilies Carcininae and certain species in the Polybiinae: i.e., rostrum directed downward, no coxal spines on legs, no sternal cornua, posterolateral spines on the fifth abdominal segment absent in both of the subfamilies, and pleopods with setal count closest to that in *Ovalipes* of the second subfamily (31–40 on the first four and ca. 22 on the uropods) (Rice and Ingle, 1975). However, the great width of the carapace sets *B. thermydron* apart.

The megalopae at first sight seem completely different from adult *B. thermydron*. While the adult is obviously specialized for life in the lightless, rift vent environment, the megalopa is seemingly less so, showing well developed though not darkly pigmented eyes, fully formed normal orbits, and some regionalization on the carapace. The shape and ornamentation of the carapace and shape of the first and third maxillipeds, however, already suggest progression toward the morphology of adult *B. thermydron* in this late larval form. Tremendous changes that occur in the orbital region and chelae during development are foreshadowed in the larger megalopae whose eyestalks are somewhat less exposed than in the smaller, and in the anterolateral margin less strongly developed in the outer orbital region. Natatory pleopods and observation from the *Alvin* by J. F. Grassle indicate weak swimming capability.

The smallest juvenile crab stages are smaller than the larger megalopae and are proportionately broader for a given length. Indeed, the length–width relationships of the juveniles, if plotted on an extension of the scatter of points shown in Fig. 8, fall directly on a straight line, indicating that there is no noticeable proportional change in body shape associated with attainment of sexual maturity (Fig. 8 was plotted before material from the late 1979 samples were received in March 1980).

The juvenile series dramatically demonstrates ontogenetic changes from late larva to adult. The ocular area becomes broadened with increasing width of the carapace, the subocular plate and epistome are gradually projected forward, and the eyestalks degenerate. The interantennular septum, completely absent in the megalopa, becomes barely visible as a minute

remnant at upper and lower edges between the two antennular fossae in the largest juvenile. General failure of this structure to develop may be functionally related to loss of sight along with heightened dependence on antennular chemoreception in a lightless environment, both this and great development of the megalopa seeming to be neotenic tendencies.

Development of marine Brachyura does not always progress through a stereotyped set of planktonic zoeal stages and single megalopa followed by staged growth into adults. Wear (1967) described the larval development of *Pilumnus lumpinus* Bennett (Xanthidae) which, in eggs 1.1 × 1.25 mm, passes through embryonic nauplius, metanauplius and complex, much modified zoea to hatch as a megalopa that swims free of the female. He contrasted this to the development of *P. novaezealandiae* Filhol whose embryonic development in eggs 1.5 × 1.4 mm passes through nauplius, metanauplius, four zoeal stages and a megalopa transition stage before hatching into a soft, flaccid megalopa which remains mostly beneath the abdomen of the female until molting to first crab stage 35 days later. The megalopa in both of these cases has a loosely flexed abdomen with biramous pleopods on abdominal segments 2–5 and short uniramous ones on the sixth segment as described above, though the number of natatory setae is fewer. Hale (1931) observed that the 1.1–1.5-mm diameter eggs of *Pilumnus vestitus* Haswell hatch directly into flaccid megalopae which remain under the abdomen of the female, molting eventually into a first crab stage which retains the megalopal abdomen and natatory hairs, but that the succeeding stage loses its pleopods completely. He reviewed published information on such degeneration of megalopal pleopods in other genera. Hale (1925) noted that *Petalomera* (=*Paradromia*) *lateralis* (Gray) (Dromiidae) hatches directly from 1.14 × 1-mm eggs into a form that can be termed a megalopa, the brood young having loosely flexed abdomen with natatory pleopods. A second stage following this, ¼ larger, had developing spines on the carapace, telson, etc., but the abdomen and pleopods were as in the first. He also judged that young of *Cryptodromia octodentata* Haswell hatch from 2-mm diameter eggs directly into miniature crabs with pleopods as above and remain in a brood under the female abdomen. Rathbun (1914) recorded abbreviated development in *Paranaxia* (=*Naxoides*) *serpulifera* (Guérin) (Majidae), the brood chamber of a female with carapace 59 mm wide containing 162 young representing two stages. The first stage had a carapace ca. 3.5 mm long, and the second ca. 5.7 mm long. Both had features of the adult and could be termed megalopae. Hyman (1924) reviewed the early work of Cano on development of *Pachygrapsus marmoratus* (Fabricius) (Grapsidae) showing that it has two megalopal stages following free swimming zoeal stages, the first with body longer than broad and forward projecting rostrum, the second relatively broader and more depressed, without projecting rostrum and with fully developed natatory pleopods as above.

Aikawa (1937) described two megalopal stages for *Plagusia dentipes* de Haan, a first that swarms in the open sea following a pelagic zoeal development, and a second that lives on weeds and timbers and exists in two forms, the second larger than the first (cl. 7.5 and 9.0 mm respectively), before transforming to first crab stage. Both megalopae have maxillae and maxillpeds of adult form and apparently natatory uropods; form a of the second stage has a projecting rostrum but b lacks it.

In contrast, Soh (1969) discussed another kind of abbreviated development in a nonmarine grapsid, *Sesarma (Geosesarma) perracae* Nobili, whose 1.6-mm diameter eggs hatch into modified zoeae which pass through a successive similar stage and then a highly modified megalopa reminiscent of a juvenile crab before becoming true juveniles. He also reviewed direct development in *Potamon* (Potamidae) (Gurney, 1942) whose females bear young crabs in the abdominal pouch. Lucas (1971) showed that species of *Halicarcinus* (Hymenosomatidae) from subtropical Australia have remarkable larval adaptations to habitat, marine and estuarine species suppressing the megalopa and a freshwater species suppressing all larval stages.

From these accounts, it is evident that representatives from six families have abbreviated larval development proceeding from rather large eggs (where egg size is recorded) and incorporating 0–2 megalopal stages. Herring (1974) examined egg sizes in a number of crustaceans, including 26 species of shrimps, 2 of galatheids, 1 polychelid, and 1 deep-sea crab (*Geryon*), finding egg sizes to vary somewhat within species and during development, large eggs having relatively high lipid content and low density when compared with small ones. He judged this relationship to be probably a consequence of abbreviated development in species with large eggs. Species with large and small eggs were found in all depth horizons; *Geryon* sp. had eggs .66 × .66 mm in diameter. *Geryon tridens* Kröyer has four zoeal and single megalopal stages (Ingle, 1979). The moderate sized eggs of *B. thermydron* (.77 × .83 mm) do not suggest storage of yolk for abbreviated development; rather, the large crablike megalopa found in the same environment may result from extension of larval development through multistaged late larvae. Such relatively inactive stages could diminish chances for dispersal away from a restricted benthic habitat.

Conclusion.—While the family Bythograeidae shares features with other brachyuran families, it fits comfortably into none of the recognized superfamilies. Therefore, the most conservative approach is to erect an independent superfamily to receive it.

Behavioral note.—During November–December 1979, observers aboard the *Alvin* noted that *B. thermydron* is distributed on hard bottom both in and well away from the warm vents, apparently not confined to the warm areas. Earlier, C-CD video tapes showed that the crabs readily move in and out of the warmed areas. Though blind, the crabs show classic brachyuran

agonistic postures such as lateral stretch of chelipeds in response to intrusion of conspecifics, or other species (a galatheid), in which smaller individuals yield to larger ones, especially in presence of bait (D. M. Cohen, personal communication). The stimulus mechanism for this remarkable behavior in blind crabs is unknown.

Literature Cited

Aikawa, H. 1937. Further notes on brachyuran larva.—Records of Oceanographic Works in Japan 9(1):87–162.

Balss, H. 1957. Decapoda. VIII. Systematik.—Bronns Klassen und Ordnungen des Tierreichs. Bd. 5, Abt. I, Buch 7, Lf. 12, pp. 1505–1672. Leipzig.

Ballard, R. D., and J. F. Grassle. 1979. Return to oases of the deep.—National Geographic Magazine 156(5):689–703.

Corliss, J. B., and R. D. Ballard. 1977. Oases of life in the cold abyss.—National Geographic Magazine 152(4):441–453.

———, J. Dymond, L. I. Gordon, J. M. Edmond, R. P. von Herzen, R. D. Ballard, K. Green, D. Williams, A. Bainbridge, K. Crane, and T. H. Van Andel. 1979. Submarine thermal springs on the Galápagos Rift.—Science 203(4385):1073–1083.

Glaessner, M. F. 1969. Decapoda.—*In* R. C. Moore (ed.), Treatise on invertebrate paleontology, Pt. R, Arthropoda 4, Vol. 2, pp. R399–R533, R626–R628, University of Kansas and Geological Society of America, Inc.

Grassle, J. F., C. J. Berg, J. J. Childress, J. P. Grassle, R. R. Hessler, H. J. Janasch, D. M. Karl, A. A. Lutz, T. J. Mickel, D. C. Rhoads, H. L. Sanders, K. L. Smith, G. N. Somero, R. D. Turner, J. H. Tuttle, P. J. Walsh, and A. J. Williams. 1979. Galápagos '79: Initial findings of a deep-sea biological quest.—Oceanus 22(2):2–10.

Guinot, D. 1968. Recherches préliminaires sur les groupements naturels chez les crustacés décapodes brachyoures. IV. Observations sur quelques genres de Xanthidae.—Bulletin du Muséum National d'Histoire Naturelle, Paris, ser. 2, 39(4) [for 1967]:695–727.

———. 1969. Recherches . . . VII. Les Goneplacidae (suite).—Ibid. 41(2):507–528.

———. 1978. Principes d'une classification évolutive des crustacés décapodes brachyoures.—Bulletin Biologique de la France et de la Belgique, NS 112(3):211–292.

Gurney, R. 1942. Larvae of decapod Crustacea.—The Ray Society, London. viii + 306 pp.

Hale, H. M. 1925. The development of two Australian sponge-crabs.—Proceedings of the Linnean Society of New South Wales 50, Pt. 4(203):405–413, pls. 39–40.

———. 1931. The post-embryonic development of an Australian xanthid crab (*Pilumnus vestitus* Haswell).—Records of the South Australian Museum 4(3):321–331.

Herring, P. J. 1974. Size, density and lipid content of some decapod eggs.—Deep-Sea Research 21(1):91–94.

Hyman, O. W. 1924. Studies on larvae of crabs of the family Grapsidae.—Proceedings of the United States National Museum 65(10):1–8, pls. 1–3.

Ingle, R. W. 1979. The larval and post-larval development of the brachyuran crab *Geryon tridens* Kröyer (Family Geryonidae) reared in the laboratory.—Bulletin of the British Museum (Natural History), Zoology 36(4):217–232.

Liddell, H. G., and R. Scott. 1940. A Greek-English lexicon, a new (ninth) edition.—Oxford University Press, London. xlviii + 2111 pp.

Lucas, J. S. 1971. The larval stages of some Australian species of *Halicarcinus* (Crustacea, Brachyura, Hymenosomatidae). I. Morphology.—Bulletin of Marine Science 21(2):471–490.

Rathbun, M. J. 1914. Stalk-eyed crustaceans collected at the Monte Bello Islands.—Proceed-
    ings of the Zoological Society of London, 1914, pp. 653–664, pls. 1–2.
Renaud, B. 1977. Les régions et les limites de la carapace d'un crustacé décapode *Carcinus
    maenas* (L.) [Brachyrhyncha Portunidae]; leurs rapports avec les systèmes fonctionels
    principaux.—Bulletin du Muséum National d'Histoire Naturelle, Ser. 3, No. 454, Zool.
    317:569–592, pls. 1–2.
Rice, A. L., and R. W. Ingle. 1975. A comparative study of the larval morphology of the
    British portunid crabs *Macropipus puber* (L.) and *M. holsatus* (Fabricius), with a dis-
    cussion of generic and sub-familial larval characters within the Portunidae.—Bulletin of
    the British Museum (Natural History), Zoology 28(4):121–151.
Soh, C. L. 1969. Abbreviated development of a non-marine crab, *Sesarma (Geosesarma)
    perracae* (Brachyura; Grapsidae), from Singapore.—Journal of Zoology 158(3):357–370.
Stephenson, W. 1972. An annotated check list and key to the Indo-West Pacific swimming
    crabs (Crustacea: Decapoda: Portunidae).—Royal Society of New Zealand, Bull. No.
    10:1–64.
———, and B. Campbell. 1960. The Australian portunids (Crustacea: Portunidae). IV. Re-
    maining genera.—Australian Journal of Marine and Freshwater Research 11(1):73–122,
    pls. 1–6.
Wear, Robert G. 1967. Life-history studies on New Zealand Brachyura. 1. Embryonic and
    post-embryonic development of *Pilumnus novaezealandiae* Filhol, 1886, and of *P. Lum-
    pinus* Bennett, 1964 (Xanthidae, Pilumninae).—New Zealand Journal of Marine and
    Freshwater Research 1(4):482–535.
Williams, A. B. 1965. Marine decapod crustaceans of the Carolinas.—Fishery Bulletin, United
    States Fish and Wildlife Service 65(1):i–xi, 1–298.

National Marine Fisheries Service, Systematics Laboratory, National
Museum of Natural History, Washington, D.C. 20560.

Addendum.—After this manuscript was sent to press, two specimens of
B. thermydron were received from J. D. Corliss, Oregon State University,
Department of Oceanography. Both specimens were collected on 16 March
1977. USNM 181292, National Geographic Camera Trap (lowered to bottom
from ship), Clambake 1, 0°47.8′N, 86°8.9′W, (depth unrecorded but approx.
2480 m), 1 ♀, cl 27.7, cw 47.2 mm; remnants of an egg clutch are among
hairs on the pleopods. USNM 181293, *Alvin* Dive 733, Garden of Eden,
0°47.69′N, 86°07.74′W, 2482 m, 1 juv., cl 6.6, cw 11.5 mm. The outline of
the juvenile carapace would slightly exceed that of Fig. 11*d* at the *a–e*
magnification; eyes of the specimen are reduced more than those outlined
in Fig. 11*b*, and are hidden under the frontoorbital border as in Fig. 11*d*.
Overall color of the juvenile is white; the slightly darkened cornea is
dorsally visible through the carapace.